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Kaasalainen, Ulla Susanna

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Standard Paper

Fossil *Usnea* and similar fruticose lichens from Palaeogene amber

Ulla Kaasalainen[1], Jouko Rikkinen[2,3] and Alexander R. Schmidt[1]

[1]Department of Geobiology, University of Göttingen, Göttingen, Germany; [2]Finnish Museum of Natural History, University of Helsinki, Helsinki, Finland and [3]Organismal and Evolutionary Biology Research Programme, Faculty of Biological and Environmental Sciences, University of Helsinki, Helsinki, Finland

Abstract

Fruticose lichens of the genus *Usnea* Dill. ex Adans. (*Parmeliaceae*), generally known as beard lichens, are among the most iconic epiphytic lichens in modern forest ecosystems. Many of the *c.* 350 currently recognized species are widely distributed and have been used as bioindicators in air pollution studies. Here we demonstrate that usneoid lichens were present in the Palaeogene amber forests of Europe. Based on general morphology and annular cortical fragmentation, one fossil from Baltic amber can be assigned to the extant genus *Usnea*. The unique type of cortical cracking indirectly demonstrates the presence of a central cord that keeps the branch intact even when its cortex is split into vertebrae-like segments. This evolutionary innovation has remained unchanged since the Palaeogene, contributing to the considerable ecological flexibility that allows *Usnea* species to flourish in a wide variety of ecosystems and climate regimes. The fossil sets the minimum age for *Usnea* to 34 million years (late Eocene). While the other similar fossils from Baltic and Bitterfeld ambers cannot be definitely assigned to the same genus, they underline the diversity of pendant lichens in Palaeogene amber forests.

Key words: Ascomycota, Baltic amber, Bitterfeld amber, lichen fossils

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Introduction

Amber is fossilized tree resin, millions to hundreds of millions of years old. The two most fossiliferous European Cenozoic ambers are Baltic and Bitterfeld amber (Dunlop 2010; Weitschat & Wichard 2010). Baltic amber, although regularly washed ashore on the coast of the Baltic Sea and the North Sea, is predominantly mined from late Eocene sediments on the Samland Peninsula near Kaliningrad (Russia) (Standke 2008). Bitterfeld amber is derived from late Oligocene strata near the city of Bitterfeld in central Germany (Knuth *et al.* 2002; Blumenstengel 2004). These ambers preserved hundreds of thousands of fossil arthropods and other animals and, as recently demonstrated, they also represent a rich source of fossil lichens (Kaasalainen *et al.* 2017*a*). Ecological interpretation of amber inclusions of various macro- and microlichens indicates that they probably originated in humid but relatively well-illuminated temperate forests (Kaasalainen *et al.* 2017*a*; Rikkinen & Schmidt 2018). This conclusion is also supported by concurrent findings from recent studies of plant inclusions, naming temperate forests as the most likely source ecosystems (Sadowski *et al.* 2017*a*, *b*, 2019).

Accurately identified lichen fossils are essential in providing independent minimum age constraints that can be used as calibration points for dating molecular phylogenies (e.g. Inoue *et al.* 2010; Lukoschek *et al.* 2012; Sauquet *et al.* 2012; Magallon *et al.* 2013). So far, four extant lichen genera have been reliably identified from Baltic and Bitterfeld ambers, namely *Anzia* Stizenb. (*Parmeliaceae*), *Calicium* Pers. (*Caliciaceae*), *Chaenotheca* (Th. Fr.) Th. Fr. (*Coniocybaceae*) and *Ochrolechia* A. Massal. (*Ochrolechiaceae*), together with the obligately lichenicolous fungus *Lichenostigma* Hafellner of the *Phaeococcomycetaceae*) (Rikkinen & Poinar 2002; Rikkinen 2003; Rikkinen *et al.* 2018; Kaasalainen *et al.* 2019; Kettunen *et al.* 2019). In addition, specimens of *Phyllopsora* Müll. Arg. (*Ramalinaceae*) have been described from Miocene Dominican amber (Rikkinen & Poinar 2008; Kaasalainen *et al.* 2017*b*). Also, several fossils of the non-lichenized but now often lichenicolous genus *Chaenothecopsis* Vain. (*Mycocaliciaceae*) have been found from both Baltic and Bitterfeld amber (Rikkinen & Poinar 2000; Tuovila *et al.* 2013; Rikkinen *et al.* 2018). Finally, many fossil macrolichens with, for example, alectorioid and parmelioid thallus morphologies and lichen-associated hyphomycetes are known from European and Dominican ambers, but most of these cannot be assigned to any fungal genus (Poinar *et al.* 2000; Kaasalainen *et al.* 2015, 2017*a*; Kettunen *et al.* 2016, 2017).

Here, we report the first fossil evidence of *Usnea*, together with other fossils of fruticose lichens from Baltic and Bitterfeld ambers. The fossils demonstrate that the genus *Usnea* existed in European amber forests and that the central cord, characteristic of all extant species, had already evolved by the Palaeogene.

Material and Methods

Fruticose lichen-forming fossils were found in three specimens of Baltic amber and in two specimens of Bitterfeld amber (Table 1).

Baltic amber originates from the Kaliningrad area (Russia) where the late Eocene sediments containing most of the amber

Author for correspondence: Ulla Kaasalainen. E-mail: ulla.kaasalainen@uni-goettingen.de

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Table 1. Fruticose lichen fossils from Baltic and Bitterfeld amber reported in this study. GZG refers to the collections of the Geoscience Centre at the University of Göttingen.

Collection number	Amber	Inclusion	Figure
GZG.BST.21943 (formerly Franziska Witsch Amber Collection, sine numero)	Baltic	*Usnea* sp.	1A & B
Carsten Gröhn Amber Collection P3675	Baltic	Fruticose lichen	2A & B
GZG.BST.21987 (formerly Jörg Wunderlich Amber Collection F2114)	Baltic	Fruticose lichen	2C
GZG.BST.21986 (formerly Heinrich Grabenhorst Amber Collection Li-110)	Bitterfeld	Fruticose lichen	2D
GZG.BST.21945 (formerly Volker Arnold Amber Collection 1768)	Bitterfeld	Fruticose lichen	2E

are 34–38 million years old, with small amounts of amber embedded in older sediments up to 48 million years old (Kosmowska-Ceranowicz *et al.* 1997; Standke 1998, 2008). Bitterfeld amber derives from the Goitzsche mine near the city of Bitterfeld in central Germany. This amber is deposited in upper Oligocene sediments with an absolute age of 25.3–23.8 million years (Knuth *et al.* 2002; Blumenstengel 2004).

Four of the fossil lichen specimens studied are kept in the collections of the Geoscience Centre at the University of Göttingen (GZG). One specimen belongs to the Carsten Gröhn Amber Collection (Glinde, Germany) which will ultimately be housed in the Geological-Palaeontological Institute and Museum of the University of Hamburg (GPIH).

The amber pieces were ground and polished manually using a series of wet silicon carbide papers (grit from FEPA P 600 to 4000, Struers Ltd) to produce smooth surfaces for investigation. Prepared amber specimens were mounted on a glass microscopic slide with the upper polished surface oriented horizontally. A drop of water was applied to the upper surface of the amber and covered with a glass coverslip to improve optical resolution for investigation and photography (Schmidt *et al.* 2012). The fossils were examined under a Carl Zeiss SteREO Discovery V8

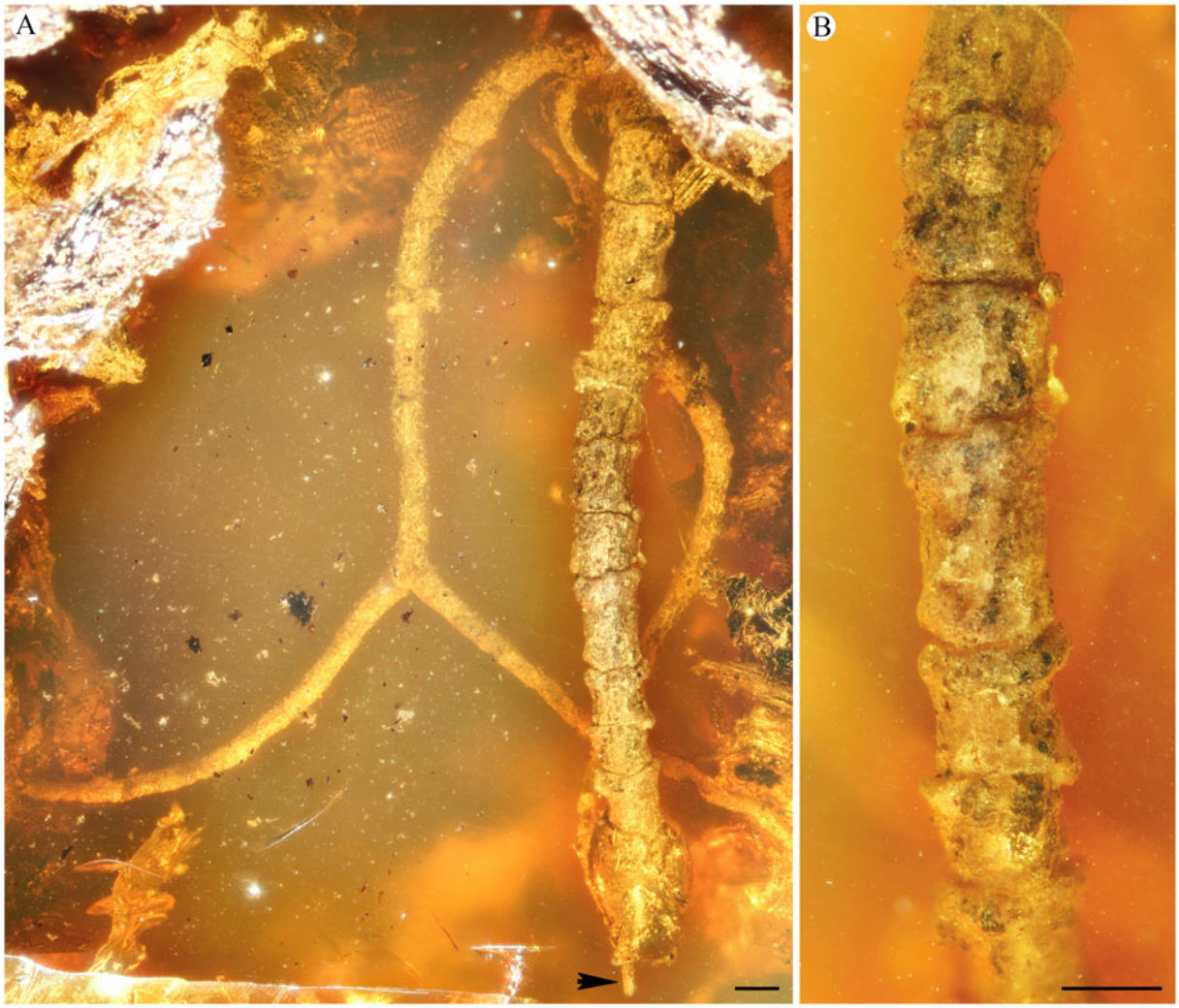

Fig. 1. Fossil *Usnea* representative in Baltic amber (GZG.BST.21943). A, fruticose thallus with terete and tapering branches. The arrowhead points to the tip of the winding side branch located behind the main branch, visible in different views of the fossil. This branch tip may erroneously suggest the presence of a cord extending from the broken main branch. B, annular cracks in the cortex divide the main branch into characteristic vertebrae-like segments. Scales = 200 μm.

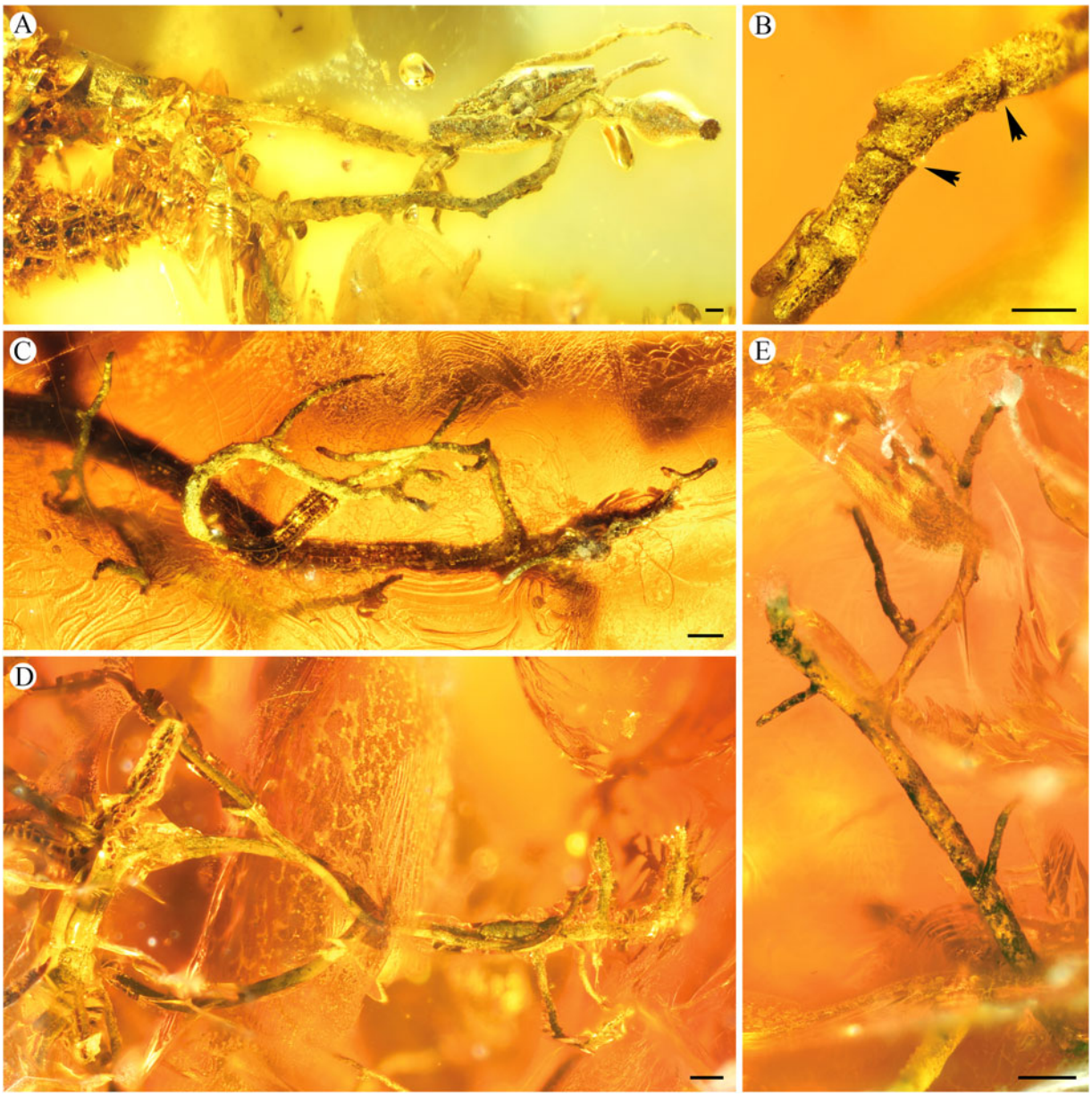

Fig. 2. Examples of further fruticose lichens in Baltic (A–C) and Bitterfeld (D & E) amber. A, overview of a putative *Usnea* in P3675. The fissures around the branches on the left-hand side of the image are a result of deterioration of the amber. B, detail of the lichen in P3675 showing cortical fragmentation (arrowheads). C, finely branched lichen in GZG.BST.21987. D, finely branched lichen in GZG.BST.21986. E, portion of a finely pendulous lichen thallus in GZG.BST.21945. Scales = 200 µm. In colour online.

dissecting microscope and a Carl Zeiss AxioScope A1 compound microscope, equipped with Canon 5D digital cameras. In most instances, incident and transmitted light were used simultaneously. For enhanced illustration of the three-dimensional inclusions, the light-microscopical images are digitally stacked photomicrographic composites made from up to 130 individual focal planes using the software package HeliconFocus version 6.3.3 Pro (Kettunen *et al.* 2019).

Results

Usnea *sp., GZG.BST.21943*

Description. The well-preserved lichen inclusion consists of one fragment of a fruticose-pendulous lichen thallus (Fig. 1A). The main branch is *c.* 5 mm long and 250–360 µm wide, and the smaller, perpendicular side branches are 100–200 µm wide, terete, tapering, with a smooth surface. Annular cortical cracks are abundantly present especially along the main branch, resulting in 230–450 µm long vertebrae-like segments that are occasionally slightly wider next to the cracking points (Fig. 1B). First cortical cracks of the side branches are formed at 110–180 µm distances.

Remarks. A very well-preserved lichen fossil showing the cortical fragmentation characteristic of many extant *Usnea* species.

Fruticose lichen, Carsten Gröhn Amber Collection P3675

Description. The lichen inclusion is well preserved, consisting of two branch tips, most probably broken off from the same thallus (Fig. 2A). Length of the inclusions is *c.* 5.5 mm; the branches are

terete and tapering, with a width ranging from 120 to 240 µm. Some cracks in the cortex are present (Fig. 2B).

Remarks. The general habit of the fossil recalls that of *Usnea* and also some cortical fragmentation is present, making the specimen a likely *Usnea* representative. The widening at the branch tip visible on the right side of Fig. 2A represents tree resin that hardened around the lichen before ultimately embedding in the larger resin body that later formed the amber specimen. The fissures around the branches on the left side of Fig. 2A are a result of deterioration of the amber around the branches.

Fruticose lichen, GZG.BST.21987

Description. Pieces of a robust fruticose-pendulous lichen thallus (Fig. 2C). Length of the main branch is *c.* 10 mm; branching mostly dichotomous; branches terete and tapering, 45–400 µm wide.

Remarks. The main branch of the fossil has almost completely deteriorated but smaller branches are better preserved. At least one cortical crack is present in the fossil.

Fruticose lichen, GZG.BST.21986

Description. Several fragments of a pendulous lichen thallus. The largest inclusion is *c.* 4.4 mm long (Fig. 2D). Side branches are terete, tapering, and 40–100 µm wide; surface faintly longitudinally striate.

Remarks. Main branches of the fossil have suffered from deterioration, but some well-preserved smaller branches exist. However, these show very few surface details.

Fruticose lichen, GZG.BST.21945

Description. Several small fragments of a finely pendulous lichen thallus (Fig. 2E). Branching dichotomous; branches terete, tapering, and 80–100 µm wide.

Remarks. The fossil has suffered from deterioration of the internal tissue, but the branching is clearly visible.

Discussion

The phylogeny and divergence of Ascomycota and especially *Parmeliaceae* have been of much recent interest (e.g. Amo de Paz *et al.* 2011; Leavitt *et al.* 2013; Beimforde *et al.* 2014; Divakar *et al.* 2017; Singh *et al.* 2018). Methods using molecular clocks to estimate divergence times of lineages rely on the few available fossils for calibration. The Palaeogene fossils of *Anzia*, *Calicium*, *Chaenotheca* and *Chaenothecopsis*, and the Miocene *Phyllopsora* (Rikkinen & Poinar 2002, 2008; Rikkinen *et al.* 2018) in particular have been used for this purpose (e.g. Beimforde *et al.* 2014; Divakar *et al.* 2017). Additionally, fossils of alectorioid lichens and '*Parmelia*' (Poinar *et al.* 2000; Kaasalainen *et al.* 2015) have been used for calibration, despite the ambiguity of their exact affiliation. More recently discovered fossils, also usable for time calibration of the evolution of lichenized fungi, include the Palaeogene *Ochrolechia* associated with the lichenicolous fungus *Lichenostigma* (Kaasalainen *et al.* 2019). As specimen GZG.BST.21943 can confidently be assigned to *Usnea*, it provides a valuable new calibration point within the *Parmeliaceae* and sets the minimum age of the genus to 34 million years.

Species of the genus *Usnea* produce fruticose shrubby to pendulous thalli with an elastic but very durable central cord. The central cord enables the formation of annular cortical fragmentation which is seen in the fossil (Fig. 1) and is also a characteristic feature of many extant species, including, for example, *U. chaetophora* Stirt. and *U. barbata* (L.) F.H. Wigg. which are common in Europe (Randlane *et al.* 2009). With *c.* 350 extant species the genus *Usnea* represents one of the most species-rich genera within the *Parmeliaceae* and the Lecanoromycetes (Thell *et al.* 2012). It has an almost worldwide distribution, with high species diversity especially in tropical and subtropical regions (Thell *et al.* 2012). Unfortunately, species delimitation within the genus is hindered by notorious morphological and chemical variation (Clerc 1998; Thell *et al.* 2012; Mark *et al.* 2016).

The extant genus *Usnea* is currently divided into three subgenera, *Eumitria* Stirt., *Dolichousnea* (Y. Ohmura) Articus and *Usnea*. The elevation of these groups to a generic level has been proposed, based on morphological differences and estimated diversification times, but this is still a matter of debate (Articus 2004; Divakar *et al.* 2017; Thell *et al.* 2018). The morphological differences include, for example, the type of central axis (tubular in *Eumitria* while solid in *Dolichousnea* and subgen. *Usnea*) and annular pseudocyphellae in *Dolichousnea* (Articus 2004). Additional differences between the groups exist, such as in cortex structure and the colour of apothecial discs (Articus 2004). However, as such features cannot be observed in the fossil, it cannot therefore be assigned into any subgroup within the genus.

According to recent phylogenetic analyses, *Usnea* forms a clade together with the monotypic genus *Cornicularia* (Schreb.) Hoffm. (Divakar *et al.* 2017; Pizarro *et al.* 2018). Based on a recent estimation, the three subgenera of *Usnea* diverged 55–30 million years ago, while *Cornicularia* was separated from *Usnea* *c.* 15 million years earlier (Divakar *et al.* 2017). The currently suggested age range of Baltic amber of 34 to 48 million years falls in this estimated divergence time. The fossil *Usnea* might thus be a member of the stem group or an early crown group representative.

Other lichen genera with a morphological resemblance to *Usnea*, historically called the usneoid lichens, include *Letharia* (Th. Fr.) Zahlbr., *Lethariella* (Motyka) Krog and *Protousnea* (Motyka) Krog. Of these, most similar is *Protousnea*. The six extant species of *Protousnea* are all confined to southern South America (Calvelo *et al.* 2005), and none of them correspond exactly with the fossilized specimens.

The thallus morphologies of the other fruticose lichens reported here vary from hair-like and probably pendulous to more robustly shrubby, but the inclusions illustrated in Fig. 2 lack defining characters or are not preserved well enough to enable accurate assignment. The two branch tips in specimen P3675 and the thallus pieces in GZG.BST.21987 resemble *Usnea* but do not possess enough characters to support a definite assignment. The inclusions in GZG.BST.21945 and GZG.BST.21986 represent pendulous and more finely branched morphologies, typical, for example, for several groups within *Parmeliaceae*, including *Alectoria* Ach., *Bryoria* Brodo & D. Hawksw., *Lethariella* and *Oropogon* Th. Fr. Similar alectorioid morphologies have also previously been described from European Palaeogene amber (Kaasalainen *et al.* 2015).

The frequent morphological convergence of many lichen groups, of which usneoid and alectorioid lichens represent prime examples, demonstrates the challenges in assigning fossil lichens to modern lineages. However, the perfectly preserved *Usnea* fossil in the amber piece GZG.BST.21943 highlights the

evolutionary endurance of the most characteristic feature in the morphology of *Usnea*: the central cord that keeps the thallus intact even when annular cracks divide the cortex into vertebrae-like segments. This evolutionary innovation has remained unaltered for at least 34 million years, contributing to the considerable flexibility in ecological adaptation, which today enables *Usnea* species to flourish in a wide variety of ecosystems and climate regimes (Gauslaa 2014; Eriksson *et al.* 2018).

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Author ORCIDs. Ulla Kaasalainen, 0000-0001-9899-4768; Jouko Rikkinen, 0000-0002-4615-6639; Alexander R. Schmidt, 0000-0001-5426-4667.

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